INVASIVE PLANTS AND FIRE: INTEGRATING SCIENCE AND MANAGEMENT

Guy R. McPherson

University of Arizona, School of Renewable Natural Resources, Biological Sciences East 325, Tucson, AZ 85721

ABSTRACT

There is great potential for integrating the science and management of fire and invasive species, but such integration faces substantial obstacles. Fundamental differences between science and management threaten the ability of scientists and managers to collaborate effectively. For example, science strives for generality, whereas management of natural resources is necessarily a site- and objective-specific endeavor. In addition, the literature on fire ecology and invasions is characterized by weak inference, relying mostly on post hoc, correlative research due to ethical and practical concerns associated with purposeful introductions. These obstacles notwithstanding, several patterns have been documented with respect to plant invasions and fire. Most notably, invasions have altered fuels, and therefore fire regimes, in many ecosystems. Grasslands characterized by frequent surface fires have been converted to shrublands and woodlands as a result of invasions by native woody plants. Concomitant alterations in fuel have decreased fire frequencies in former grasslands, and have contributed to high-intensity crown fires in some woodlands. Fire can also facilitate plant invasions by reducing interference from native species and increasing availability of soil nutrients. Invasions by nonnative grasses in former shrublands of Hawaii and deserts of the American Southwest promote recurrent fires that lead to increased dominance of these grasses and the establishment of grass–fire cycles. Unfortunately, documenting rates and patterns of spread has provided little predictive power and few clues about control strategies. It is clear, however, that predicting and controlling the spread of invasive species will require a concerted, holistic effort that integrates science and management. In addition, fire and invasive species should not be managed independently, but should be integrated into a coherent management strategy.

keywords: ecosystem function, fire, plant invasions, resource management, science, structure.

Citation: McPherson, G.R. 2001. Invasive plants and fire: integrating science and management. Pages 141–146 in K.E.M. Galley and T.P. Wilson (eds.). Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

INTRODUCTION

Great potential exists for integrating the science and management of fire and invasive species. Fire represents an important ecological process and a powerful management tool, and biological invasions may teach us a lot about ecology while presenting fascinating challenges for management. A few decades ago, purposeful introductions of some invasive species were crowning achievements of collaborative efforts between ecologists and managers. Many of these species now offer superb opportunities for scientists and managers to work together again for the benefit of society as they did a few decades ago. Lehmann lovegrass (Eragrostis lehmanniana), for example, was introduced to the southwestern United States during the early 1930s after a worldwide search for a species that would establish on sites denuded by livestock grazing and characterized by low and variable annual precipitation. Its introduction was a significant accomplishment 7 decades ago, but now this species is viewed as a threat to biological diversity (Bock et al. 1986). As such, identification of a control strategy represents a formidable challenge—and an opportunity for collaboration—for natural resource managers and ecologists.

The ability to integrate ecology and management is not without obstacles. Science strives for generality: scientists seek laws, predictions, and explanations with maximum applicability. In contrast, management of natural resources is necessarily a site- and objectivespecific endeavor that often is conducted within a localized cultural arena. As a result, management actions that are effective for a specific objective, species, and site may be ineffective or inappropriate for another objective, species, or site. Further, social, political, or economic factors often constrain management actions, even in the seemingly narrow subdisciplines of plant invasions and fire ecology. Management of fire and invasions is strongly influenced by human values, whereas scientists seek logic and facts that are independent of human values.

ECOLOGY AS A BASIS FOR MANAGEMENT: PROMISES AND CONSTRAINTS

Ecology is the scientific study of the abundance and distribution of organisms (definition adapted from Krebs 1995). Natural resource management is an attempt to control the distribution and abundance of various organisms to meet societal needs. This is particularly obvious in the case of invasive species, which, depending on societal needs perceived by managers, may be purposefully introduced or may be the target of control efforts. In several instances, the purposeful introduction of nonnative plants has been followed by efforts to control the species a few decades later. Thus,

142 McPHERSON

human values change over time, and managers are expected to respond quickly. The discipline of ecology, in turn, should provide a firm scientific foundation for managing natural resources. As such, the vast and growing ecological literature should serve as a reservoir of information for those entrusted with management of natural resources (McPherson and Weltzin 2000).

Clearly, however, ecology has not always served managers well. Ecological science has several characteristics that make it easy to ignore, and much research on fire and invasions has been conducted in a manner that encourages misuse. Contemporary debates in conservation biology, wildlife ecology, range science, and forestry, as well as in policy-making bodies at state and national levels, indicate that knowledge derived from science is often ignored or marginalized or is too rudimentary or too general to aid managers. Rather than relying on science to make decisions, managers—and the public they represent—often base management decisions on tradition, organizational culture, emotion, or personal values.

Why do managers seem to ignore science? The public is generally skeptical of science, perhaps in part because ecology is often confused with environmentalism, and environmental activists typically are viewed as extremists. However, natural resource managers generally have a background in science (although it could be argued that this background is not sufficiently developed with respect to experimental design, statistical analyses, and philosophy of science). Therefore, they should be able to recognize and value scientific contributions, as well as distinguish ecology from environmentalism. Thus, other attributes of contemporary ecology must contribute to its lack of acceptance by natural resource managers and lack of impact on management. I suggest that the major limitation is weak inference (sensu Platt 1964). Much of the literature on fire ecology is descriptive and therefore non-mechanistic, although experimental research has been employed in a few systems (e.g., Glitzenstein et al. 1995, Platt et al. 1988, Ford and McPherson 1998). Similarly, the study of biological invasions is reliant on post hoc, correlative research due to ethical and practical concerns associated with purposeful introductions. In contrast, experimental research on control measures for invasive species is minimally constrained by ethical or practical issues, and results of control efforts are scattered through the ecological literature. In addition, managers have conducted considerable experimental research on control of invasive plants (i.e., trial and error); unfortunately, most of these results are not readily accessible in the broad literature. Thus, there is a paucity of published experimental research on both fire and biological invasions. More importantly, I know of no published experimental research on interactions between fire and invasive species, with the exception of the few studies that used fire as a potential control measure.

The non-mechanistic nature of much ecological research and the extensive ecological literature make it easy for even conscientious managers to select evidence subconsciously to support their views while ignoring other evidence. Thus, the ecological literature often serves as a source of justification for management actions, not as a guide for unbiased decision-making. In effect, the descriptive nature of most published ecological research encourages managers to pick and choose from the ecological literature (Mc-Pherson 1997).

In addition to weak inference associated with research on fire and invasions, such research is characterized by case-studies with limited applicability beyond the local site. Further, many study sites are selected specifically because they appear to be minimally impacted by prior management, which limits application (McPherson 1997). Case-studies, including socalled "natural" experiments (sensu Diamond 1983), are valuable sources of local information. However, extrapolation beyond the area in which these studies are conducted should be done only with extreme caution, and literature derived from these observations seems unlikely to generate broad-scale principles that will guide management. Finally, few experiments on fire and invasions have been conducted at scales appropriate to management. Experimental research is nearly always restricted to much smaller areas than the fundamental units of management, and there are significant barriers to scaling up from small quadrats to watersheds. Substantial progress is being made on issues of scale, and fire ecologists are increasingly conducting experiments at temporal and spatial scales more appropriate to management. However, much progress remains to be made before ecological studies of invasions or interactions between fire and invasions are generally applicable to management efforts.

Ecosystems change over time, and this confounds attempts to conserve them and complicates attempts to monitor them. Consider, for example, the conversion of grasslands to woodlands or forests during the past few centuries. Ecologists have documented this phenomenon in many former grasslands throughout the world (reviewed by Archer 1995), and they have strived to convince the general public and natural resource managers that we need to know why the conversion occurred, and whether reintroduction of pre-European fire regimes will reverse the process of woody plant encroachment. Consistent with the goal of providing explanations for ecosystem response to manipulations or natural phenomena, ecologists have proposed hypotheses to account for the increased abundance of invasive woody plants in former grasslands. The most widely accepted hypothesis is that woody plants have encroached as a result of post-European livestock grazing and a concomitant decrease in fire frequency within the context of periodic droughts (e.g., Wright and Bailey 1982, Bahre 1991, McPherson 1997). This hypothesis may be correct, and it has become reified in the literature (sensu Slobodkin 2001). As with many retrospective hypotheses, however, it cannot be tested.

The scientific method uses observations to generate hypotheses, then explicit tests of hypotheses, usually via experimentation. This approach reflects the

contemporary philosophical view that hypotheses are candidate explanations for patterns observed in nature (Medawar 1984). Ecologists have appropriately used historical data to describe the pattern of an increase in woody plants within former grasslands (e.g., Buffington and Herbel 1965, Progulske 1974, Burkhardt and Tisdale 1976, Gruell 1983, Humphrey 1987, Archer 1995). However, many ecologists have then inappropriately used the historical data—which formed the basis for the hypothesis—to "test" the hypothesis. This circular, retrospective approach is characterized by weak inference and a "test" that is neither independent nor rigorous. For example, the generally accepted hypothesis regarding woody plant invasion may be incorrect: alternative explanations such as episodic precipitation events, altered temperature regimes, increased concentrations of atmospheric CO₂, anthropogenically enhanced seed dispersal of woody plants, or other factors that may play pivotal roles in the conversion of grasslands to woodlands cannot be ruled out. Unfortunately, many such retrospective hypotheses simply are not testable (McPherson 1997, 2001).

Additionally, accurate reconstruction of events that contributed to historical changes in vegetation will not necessarily facilitate contemporary management. Pervasive and profound changes have occurred in the biological and physical environments during the last century (e.g., dominance of many sites by nonnative species, altered levels of livestock grazing, increased concentrations of atmospheric CO₂). As a result, understanding the past will not ensure that we can predict the future. In fact, such understanding may impede contemporary management by lending a false sense of security to predictions based largely on retrospection. Just as we would never drive an automobile by looking primarily in the rear-view mirror, we should not expect retrospective analyses to provide much meaningful information for management of contemporary ecosystems (McPherson 1997).

Experimentation offers a partial solution to the problem of prediction. Specifically, manipulation of relevant biotic and abiotic factors at scales applicable to management can provide the foundation for predicting near-future changes in ecosystems. In the past, poorly designed experiments with limited applicability to management have contributed to a perception that the experimental approach is flawed. Although individual experiments may be flawed, experiments are the only consistently reliable means of determining mechanisms of vegetation change. I believe that managers can contribute to scientific inquiry in the following ways: (1) posing tractable questions, (2) helping to design ecological experiments, (3) seeking management implications from published research, (4) understanding the difference between hypotheses and predictions, (5) understanding weak inference, (6) assessing experimental techniques and research methods, and (7) facilitating insightful research experiments on lands within their jurisdiction.

Although I strongly encourage an experimental approach to ecology and resource management, I do not advocate reductionism in either the science or man-

agement of fire and invasive species. To the contrary, approaching fire and invasive species in a strictly reductionist manner invites failure on 3 fronts: (1) controlling invasive species, (2) understanding systems and species, and (3) linking ecology and management. Each of these issues is important to ecology, management, and society. Collectively, they argue for the use of multiple approaches in the development and application of knowledge on fire and invasive species. These approaches must be holistic to incorporate all relevant information, and they must rely on observations, descriptions, comparisons, and experiments. Additionally, the use of fire as a potential control measure must be integrated with other tools (e.g., herbicides, biological control). However, meaningful and longlasting progress toward pluralism can be achieved only via the generation and application of reliable knowledge (sensu Romesburg 1981).

In addition to experimentation, ecology offers numerous tools that may be used to evaluate the success of management actions. The ecological literature is replete with monitoring protocols and analytical techniques that have been developed for assessing ecosystem structure and function (e.g., Bonham 1989, Kent and Coker 1992). Monitoring efforts will be effective only to the extent that they are based on measurable, clear objectives (e.g., to identify changes in species composition over time). Data derived from monitoring will be useful if they are based on structural and functional attributes, rather than poorly defined non-concepts such as ecosystem "health," "integrity," and "sustainability" (in the absence of specifying what is being sustained) (Wicklum and Davies 1995, Lélé and Norgaard 1996, McPherson 1997).

Finally, scientists can facilitate management via several specific means. They can focus on questions that address important management issues within the context of a mechanistic program of research. They can synthesize relevant findings from their research and research conducted by other scientists. They can supply information in outlets accessible to managers, and they can respond to requests for information and advice in a timely and thoughtful manner.

PLANT INVASIONS AND FIRE: A SUMMARY

The invasion of a plant into a matrix of species with which the invader has not evolved is, by definition, a unique event. As such, variations in invader species, the invaded system, and interactions between the species and the system pose serious challenges to summarizing the vast and expanding literature on plant invasions and fire. Plant invasions alter the structure and function of ecosystems in myriad ways, and many of the alterations influence fire regimes and post-fire response. Therefore, this summary will focus on impacts of plant invaders on fuels and fire regimes.

Invasion of former grasslands in North America by woody plants, many of which are native to the region, typically suppresses herbaceous production (re144 McPHERSON

viewed by McPherson 1997). In the absence of woody-plant invasion, these grasslands support frequent, low-intensity surface fires. The reduction in fine fuel associated with invasion by woody plants typically makes these sites less flammable, at least in the short term (McPherson 1995, 1997). If woody angiosperms such as mesquite (*Prosopis* spp.) or creosotebush (Larrea tridentata) dominate the overstory, sites often will not support fire spread. Rather, control of these woody invaders must be accomplished with mechanical or chemical methods. Invasion and subsequent dominance of the overstory by woody gymnosperms (pine [Pinus spp.], juniper [Juniperus spp.]) usually has a similar effect, at least initially: decline of herbaceous plants in the understory reduces the probability of fire spread. Continued development of the overstory, coupled with a hot, dry period that reduces moisture content of overstory plants, contributes to increased probability of fire. The resulting fires are high-intensity crown fires quite unlike the low-intensity surface fires that characterized these systems before woody-plant invasion. Thus, at a coarse level of resolution, invasion of former grasslands by woody plants fundamentally changes the fire regime in 1 of 2 ways: relatively frequent, low-intensity surface fires are replaced by (1) infrequent, high-intensity fires or (2) no fires.

Invasion of grasslands by nonnative grasses with different physiologies or phenologies from dominant native plants may alter fire regimes in relatively subtle ways. For example, nonnative grasses with the C_3 photosynthetic pathway have invaded many temperate grasslands formerly dominated by C_4 grasses (Sims 1988, Wedin 1995, Smith and Knapp 1999), thereby increasing the availability of fine fuel early during the year and altering the season during which fires are likely to spread. Prescribed fires can be used to manipulate the ratio of C_3 and C_4 plants in these grasslands (Sims 1988, Steuter and McPherson 1995).

Invasion of shrublands or woodlands by grasses (e.g., downy brome [Bromus tectorum] into sagebrush [Artemisia spp.] communities, Mediterranean annual grasses into creosote communities, African grasses into Hawaiian woodlands), most of which are not native to North America, increases herbaceous production. Increased fine fuels associated with nonnative perennial grasses are slow to decompose in western North America, and therefore persist for several years. In contrast, the increased fine fuel associated with nonnative annual grasses is often episodic and transient. For example, Mediterranean annual grasses occur infrequently in the shrub-dominated Sonoran Desert except when autumn and winter rains are sufficient to stimulate their germination and survival (Brown and Minnich 1986, Abbott and McPherson 1999). During these years, which typically correspond to the El Niño Southern Oscillation, annual grasses form a continuous layer of fine fuel on the desert floor. Regardless of whether the "pulse" of fine fuel is persistent (perennial grasses) or ephemeral (annual grasses), the usual consequence is relatively frequent surface fires in systems that historically burned rarely or never. Because fires typically favor the nonnative grasses that serve as the fuel, a positive feedback develops (the "grass-fire cycle" of D'Antonio and Vitousek 1992; also see D'Antonio et al. 2001). Native plants in these systems evolved in the absence of periodic fires; as a result, fire-induced mortality of woody plants and succulents may be very high. One potential solution in areas dominated by annual grasses is to allow livestock to graze intensively for a few weeks when grasses are palatable, thereby reducing the fine fuel (Abbott and McPherson 1999). Such use of nonnative species (livestock) to reduce the potential impacts (fire-induced mortality of native perennial plants) of other nonnative species (annual grasses) has been widely used on noxious herbaceous dicots, but not on grasses (Sheley and Petroff 1999).

MANAGING IN THE FACE OF COMPLEXITY

Science has illustrated the complexity of the natural world. Labyrinthine interactions between plants, animals, soils, climate, and land use drive these complex dynamics. A rapidly developing ecological literature challenges static equilibrium models: rapid biological invasions and response of plant communities to fire are described within the context of non-equilibrium communities (e.g., using state-and-transition models, sensu Westoby et al. 1989). However, the language, concepts, models, and theories found in the ever-expanding ecological literature threaten to overwhelm even the most dedicated managers.

In the face of this complexity, managers have tried to simplify: limits on human cognition and relatively "simple" management objectives have encouraged managers to develop "simple" solutions. "Simple" management objectives, such as food and fiber production, will continue to dominate many areas. (In most cases, neither the objective nor the solution is simple; both, however, appear simple relative to objectives and solutions managers will face in the near future.) The annual growth rate of the global human population is nearly 1.5%, and this ensures a continuing demand on natural resources to meet basic human needs (Ehrlich and Ehrlich 1990, Daily and Ehrlich 1996). This human population growth is not merely a concern for intensively managed lands. Our increasing presence and consumptive and non-consumptive demand for resources threaten every natural area and resource.

For example, the annual net primary productivity that is used directly, co-opted, or foregone because of human activities has risen from 1% to 40% within the last 2 centuries (Vitousek et al. 1986). In contrast, the fraction of production left for other organisms on the planet has dropped from 99% to 60%, and it continues to decline (Vitousek et al. 1986). Human-caused extinction of many species seems inevitable in light of exponential population growth. We can document the losses, but we cannot continue to increase at an exponential rate and conserve all remaining taxa.

Managers must grapple with the complexity of managing for multiple uses and satisfying many users. In the case of fire and biological invasions, sciencebased stewardship is constrained, in part, by ecological knowledge that is characterized by weak inference. I suggest that the enormity, complexity, and importance of management make the creative application of existing knowledge as important, and as difficult, as the development of new knowledge. This challenge can be addressed, in part, by identifying management practices that are based on knowledge derived from weak inference. Further, identification of these management practices reveals an opportunity for cooperation between scientists and managers: "conventional wisdom" can be reevaluated with rigorous experimental protocols.

Natural resource managers have a crucial role in the conservation of natural ecosystems, if only because they are accountable and responsible for their decisions to a far greater extent than scientists. The decisions they make regarding which pieces of information to apply to site-specific management will have farreaching and lasting consequences. These decisions are based on human values, some of which change periodically: consider the many nonnative species purposefully introduced into North America now viewed as threats. Science alone cannot determine what should be conserved, and science generally attempts to free itself from judgments based on values (Lawton 1997). Thus, decisions about what to conserve, and how best to practice conservation, must be made by managers in light of societal demands. An observation of E.O. Wilson (1998:294) applies to natural resource managers: "We are drowning in information, while starving for wisdom. The world henceforth will be run by synthesizers, people able to put together the right information at the right time, think critically about it, and make important choices wisely."

As decision-makers, managers must synthesize disparate information for practical use, and they must rely on all relevant knowledge. They must make a concerted effort "to put together the right information at the right time, think critically about it, and make important choices wisely" (Wilson 1998:294). Further, they must make these choices swiftly and implement them forcefully in a site-specific and objective-specific manner—a formidable challenge indeed.

ACKNOWLEDGMENTS

I thank E.L. Geiger, L.F. Salo, K.A. Snyder, H.R. Taylor, J.F. Weltzin, and 2 anonymous reviewers for reviewing early drafts of the manuscript and Matt Brooks for inviting and facilitating my participation in Fire Conference 2000.

LITERATURE CITED

Abbott, L.B., and G.R. McPherson. 1999. Nonnative grasses in southern Arizona: historical and contemporary perspectives. Pages 3–6 *in* L. Benson and B. Gebow (eds.). A century of parks in southern Arizona: second conference on research

- and resource management in southern Arizona National Parks, extended abstracts. National Park Service and U.S. Geological Survey Sonoran Desert Field Station, University of Arizona, Tucson.
- Archer, S. 1995. Tree–grass dynamics in a *Prosopis*–thornscrub savanna parkland: reconstructing the past and predicting the future. Écoscience 2:93–99.
- Bahre, C.J. 1991. A legacy of change: historic human impact on vegetation of the Arizona borderlands. University of Arizona Press, Tucson.
- Bock, C.E., J.H. Bock, K.L. Jepson, and J.C. Ortega. 1986. Ecological effects of planting African lovegrasses in Arizona. National Geographic Research 2:456–463.
- Bonham, C.D. 1989. Measurements for terrestrial vegetation. Wiley-Interscience, New York, NY.
- Brown, D.E., and R.A. Minnich. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. American Midland Naturalist 116:411–422.
- Buffington, L.D., and C.H. Herbel. 1965. Vegetational changes on a semi-desert grassland range from 1958 to 1963. Ecological Monographs 35:139–164.
- Burkhardt, J., and E.W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57:472–484.
- Daily, G., and P. Ehrlich. 1996. Socioeconomic equity, sustainability, and Earth's carrying capacity. Ecological Applications 6:991–1001.
- D'Antonio, C.M., R.F. Hughes, and P.M. Vitousek. 2001. Factors influencing dynamics of two invasive C_4 grasses in seasonally dry Hawaiian woodlands. Ecology 82:89–104.
- D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.
- Diamond, J.M. 1983. Laboratory, field and natural experiments. Nature 304:586–587.
- Ehrlich, P., and A. Ehrlich. 1990. The population explosion. Simon & Schuster, New York, NY.
- Ford, P.L., and G.R. McPherson. 1998. Experimental fire research in semi-arid shortgrass prairie. Pages 107–116 in B. Tellman, D.M. Finch, C. Edminster, and R. Hamre (eds.).
 The future of arid grasslands: identifying issues, seeking solutions. Proceedings RMRS-P-3, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Glitzenstein, J.S., W.J. Platt, and D.R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65:441–476.
- Gruell, G.E. 1983. Fire and vegetative trends in the northern Rockies: interpretations from 1981–1982 photographs. General Technical Report INT-158, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.
- Humphrey, R.R. 1987. 90 years and 535 miles: vegetation changes along the Mexican border. University of New Mexico Press, Albuquerque.
- Kent, M., and P. Coker. 1992. Vegetation description and analysis: a practical approach. CRC Press, Boca Raton, FL.
- Krebs, C.J. 1995. Ecology: the experimental analysis of distribution and abundance. Fourth edition. Harper & Row, New York, NY.
- Lawton, J.H. 1997. The science and non-science of conservation biology. Oikos 79:3–5.
- Lélé, S., and R.B. Norgaard. 1996. Sustainability and the scientist's burden. Conservation Biology 10:354–365.
- McPherson, G.R. 1995. The role of fire in desert grasslands. Pages 130–151 *in* M.P. McClaran and T.R. Van Devender (eds.). The desert grassland. University of Arizona Press, Tucson.
- McPherson, G.R. 1997. Ecology and management of North American savannas. University of Arizona Press, Tucson.
- McPherson, G.R. 2001. Teaching and learning the scientific method. American Biology Teacher 63:242–245.

McPHERSON

McPherson, G.R., and J.F. Weltzin. 2000. Disturbance and climate change in U.S./Mexico borderland plant communities: a state-of-the-knowledge review. General Technical Report RMRS-GTR-50, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins,

- Medawar, P. 1984. Pluto's republic. Oxford University Press, New York, NY.
- Platt, J.R. 1964. Strong inference. Science 146:347-353.
- Platt, W.J., G.W. Evans, and M.M. Davis. 1988. Effects of fire season on flowering forbs and shrubs in longleaf pine forest. Oecologia 76:353–363.
- Progulske, D.R. 1974. Yellow ore, yellow hair, yellow pine: a photographic study of a century of forest ecology. South Dakota State University Agricultural Experiment Station Bulletin 616, Brookings, SD.
- Romesburg, H.C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management 45:293–313.
- Sheley, R.L., and J.K. Petroff. 1999. Biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis.
- Sims, P.L. 1988. Grasslands. Pages 265–286 in M.G. Barbour and W.D. Billings (eds.). North American terrestrial vegetation. Cambridge University Press, Cambridge, United Kingdom.

- Slobodkin, L.B. 2001. The good, the bad and the reified. Evolutionary Ecology Research 3:1–13.
- Smith, M.D., and A.K. Knapp. 1999. Exotic plant species in a C₄-dominated grassland: invisibility, disturbance, and community structure. Oecologia 120:605–612.
- Steuter, A.A., and G.R. McPherson. 1995. Fire as a physical stress. Pages 550–579 *in* D.J. Bedunah and R.E. Sosebee (eds.). Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver. CO.
- Vitousek, P.M., P.R. Ehrlich, A.H. Ehrlich, and P.A. Matson. 1986. Human appropriation of the products of photosynthesis. BioScience 36:368–373.
- Wedin, D.A. 1995. Species, nitrogen, and grassland dynamics: the constraints of stuff. Pages 253–262 in C.G. Jones and J.H. Lawton (eds.). Linking species & ecosystems. Chapman & Hall, New York, NY.
- Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266–274.
- Wicklum, D., and R.W. Davies. 1995. Ecosystem health and integrity? Canadian Journal of Botany 73:997–1000.
- Wilson, E.O. 1998. Consilience: the unity of knowledge. Alfred A. Knopf, New York, NY.
- Wright, H.A., and A.W. Bailey. 1982. Fire ecology, United States and southern Canada. Wiley-Interscience, New York, NY.

146